

On the Development of the Segments of the Head in Scyllium.

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With Plates 1 and 2 and 1 Text-figure.

THE object with which this work was undertaken was to describe the development of the skull in Scyllium and the relation of its elements to the general segmentation of the head, more especially in the occipital region. But it soon became evident that our knowledge of the segmental composition of the head in Elasmobranchs is still in a very unsatisfactory condition, and that a re-investigation of the whole question was necessary. In addition, then, to an account of the development of the skeletal segments, a short history of the mesoblastic somites is given, and incidentally of certain points in the development of the nerves and other structures in the head region.

In embryological investigations it is most essential to have as complete a series of stages as possible; most of the results recorded below have been reached with the help of careful graphic reconstructions of longitudinal sections from 10 to 15 μ thick in my possession; but I have also, through the kindness of Mrs. Jenkinson, had the privilege of making use of many series, especially of the early stages, in the collection of the late Capt. J. W. Jenkinson; and to Prof. J. P. Hill I am indebted for the loan of certain stages.

The foundation of our knowledge of the segmentation of the head of the Elasmobranch on embryological evidence was laid by Balfour in his epoch-making researches published in the years 1876-7-8 (2). Some of his results had already appeared in a preliminary note in 1874 (1), and in the later work he described the subdivision of the mesoblast of the head and its *cœlom* by the visceral clefts, and the development of cranial nerves 5, 7, 8, 9 and 10, which "all develop precisely as do the posterior roots of the spinal nerves." He further showed that each mesoblastic segment is related to a nerve running behind it, that its splanchnopleure gives rise to visceral muscles, and suggested that the pre-mandibular somite gives rise to some of the muscles of the eye. "The morphological importance of the sections of the body-cavity in the head," says Balfour, "cannot be overestimated and the fact that the walls become developed into the muscular system of the head renders it almost certain that we must regard them as equivalent to the muscle plates of the body, which originally contain, equally with those of the head, sections of the body-cavity." They therefore "serve as valuable guides to the number of segments which have coalesced to form the head," and there are "a pair of these head-cavities in front of the mandibular arch, a pair in the mandibular arch, and a pair in each succeeding arch. In all there are eight pairs of these cavities representing eight segments, the first of them preoral." No better or more convincing statement of the embryological evidence of the segmentation of the head could be wished, and the quotations are given in full because in many recent reviews of the literature the importance of the work of Balfour seems to me to have been somewhat underestimated. His tabular statement is given below, and it may be said at once that the best and most recent work has fully confirmed his main conclusions. All the many attempts made to prove that there are more or fewer segments embodied in the region of the head there dealt with may be said to have failed.

Table of the Cephalic Segments as determined by the Nerves, Visceral Arches, and Head-cavities (Balfour, 2).

Segments.	Nerves.	Visceral arches.	Head-cavities or cranial muscle-plates.
Preoral 1 .	3rd and 4th and ? 6th nerves (perhaps representing more than one segment)	?	1st head-cavity
Postoral 2 .	5th nerve	Mandibular	2nd head-cavity
" 3 .	7th nerve	Hyoid	3rd " "
" 4 .	Glosso-pharyngeal nerve	1st branchial arch	4th " "
" 5 .	1st branch of vagus .	2nd " "	5th " "
" 6 .	2nd " "	3rd " "	6th " "
" 7 .	3rd " "	4th " "	7th " "
" 8 .	4th " "	5th " "	8th " "

Shortly afterwards appeared the work of Marshall (18) who emphasised the comparison between the more dorsal truly segmented somites with their head-cavities and the more ventral region in the arches with the somites and lateral plate in the trunk. The segmentation of the "head-cavities" dorsally is really independent of the visceral clefts. He further traced the origin from the premandibular somite of the four muscles supplied by the oculo-motor nerve and the origin of the rectus externus from a more posterior segment which he rightly supposed to be the third head-cavity supplied by the abducens nerve. Moreover, he identified this nerve as the ventral root of the facial.

The next important contribution came from van Wijhe in 1882 (26). He described in detail the development and fate of the eight head segments discovered by Balfour. A typical head-segment contains on each side, according to van Wijhe, a somite (myotome and sclerotome) below which extends the cavity of a visceral arch, and a visceral cleft. Related to each such segment is a dorsal and a ventral nerve root; these remain separate from each other, just as they have been shown by Balfour to be in early stages in the trunk, and as

they remain permanently in *Amphioxus*. The dorsal ganglionated root supplies the musculature derived from the lateral plate mesoblast, while the ventral root supplies the muscles developed from the segmental myotome. The "ciliary ganglion" of Marshall was identified by van Wijhe as belonging to the ophthalmicus profundus, the dorsal root of the first or premandibular segment; the third, fourth, and sixth cranial nerves as the ventral roots of the first three or pro-otic segments. Further, he definitely traced the development of the eye-muscles from the corresponding three myotomes, and the origin of the hypoglossal roots from the hinder meta-otic segments of which the vagus represents the dorsal roots only.

Van Wijhe, however, attributed nine segments to the head; the tenth segment, in which a typical spinal ganglion and mixed nerve develops, he considered to belong to the trunk. There is, however, an unfortunate discrepancy between the results of Balfour and van Wijhe which, in spite of the great value of the latter's work, seems to have led to a deal of unnecessary confusion and controversy.¹ For while van Wijhe describes and figures somites 3 to 8 as lying one above each of the six gill-slits, with the seventh, ninth, and four branches of the tenth nerve corresponding in the same way to slits and arches, he assumes, for reasons which are by no means clear and on what seems to me quite insufficient evidence, that the fourth somite belongs to the hyoid arch in front of it and not to the first branchial below and behind it. Now since the third somite obviously belongs to the hyoid segment and is continued below into the mesoblast and cavity of the hyoid arch, van Wijhe's interpretation leaves the

We need not enter here into an account of the long controversies carried on by Kastschenko, Killian, Dohrn, Rabl, Froriep, and others, as to the segmental and somitic nature of the head-somites mentioned above. That these somites produce muscles from their inner walls and are serially homologous with the trunk myotomes seems to have been clearly established by the work of Killian, Platt, Hoffmann, and Neal. A good discussion with full references to the literature will be found in Neal's papers (19, 20).

fourth somite without corresponding slit, arch, or nerve, either in the embryo or in the adult. His assumption that these have disappeared seems both unjustified and unnecessary; so far as I am aware, no serious evidence of their presence has ever been found in spite of the fact that many investigators have sought for them. This view of van Wijhe, which would upset the orderly arrangement of gill-slits, somites, and nerves as set forth in Balfour's scheme, has been adopted in a more or less modified form by various later authors, for instance, by Miss Platt (21), Neal (19), Sewertzoff (25), and Braus (3). But it is not supported by Ziegler's observations on *Torpedo* (28), and is totally at variance with the excellent work of Koltzoff on *Petromyzon* (17), according to whom a somite, a dorsal and ventral nerve root and a visceral arch are present in every segment of the head from the mandibular to the most posterior. Johnston, in his valuable paper on the "Morphology of the Vertebrate Head" (16), adopts Koltzoff's results.

The Relation of the Nerves to the Myotomes.—Before attempting to enumerate the segments of the head it is very important to determine, if possible, the exact relation of the nerves to the myotomes and scleromeres in the trunk.¹

Neal, in his important paper on the "Development of the Nervous System of *Squalus*" (*Acanthias*) concludes that the segmental dorsal roots are originally intersomitic, thus agreeing with Balfour. Hatschek had pointed out that in *Amphioxus* and *Petromyzon* the dorsal roots are septal; that is to say, run out in the septa between the myotomes (13). Now, in all other Craniate Vertebrates the dorsal roots shift somewhat in position and join with the ventral roots to form mixed spinal nerves, and the question arises as to whether a dorsal root and its ganglion combine with the ventral root behind or with the ventral root in front. The ventral roots themselves

¹ While the terms "myotome" and "myomere" are practically synonymous, the word "scleromere" is here used to signify the axial skeletal element of a segment derived from an earlier sclerotome which may also give rise to connective tissue and other parts.

are undoubtedly intrasomitic; that is to say, at first pass directly outwards from the nerve cord to the middle of the somite they supply, as was long ago shown by Balfour. Between successive myotomes pass out sclerotome cells to form the septum, and along the posterior face of this septum run vertically upwards the intersomitic segmental vessels, arteries and veins, from the dorsal aorta and cardinal veins. This disposition is constant throughout the Gnathostomes in the embryo, and is found to persist in the adult *Petromyzon*. Hatschek (13), when comparing the *Ammocoete* larva with *Amphioxus*, first concluded that a dorsal root really belongs to the ventral root in front of it. But soon after he changed his mind, and concluded that in Craniates the dorsal root becomes associated with the ventral root of the myotome lying behind it (14). The evidence on which he based his opinion is not clear, and it is obvious that if the roots combined according to the later suggestion they would embrace the segmental vessels between them.¹

An examination of a complete series of stages of *Scyllium* embryos, cut in horizontal as well as vertical longitudinal sections, demonstrates conclusively that the rudiment of the spinal ganglion takes up a position from the first opposite the myotome, but near its hinder edge (Pl. 2, figs. 20-24). The sclerotome and scleromere tissue develops chiefly between adjacent myotomes, passing obliquely backwards and outwards to form the future septum and rib, while the main branch of the nerve coming from the ganglion also passes out to the skin behind the myotome (Pl. 2, fig. 45) (9). We are, therefore, justified in concluding that in the Gnathostomes the

¹ In Myxinoids (*Myxine* and *Bdellostoma*) I find that the segmental vessels pass up between the anterior ventral and posterior dorsal roots of each spinal nerve. Prof. F. J. Cole has very kindly provided me with a reconstruction from sections of *Myxine* which confirms my observation on dissections. This exceptional disposition would suggest that the roots have combined in some way differing from that which obtains in the Gnathostomes, and would thus support the view, put forward by Koltzoff, that the mixed spinal nerve of the Myxinoids has been formed independently of that of the Gnathostomes.

position taken up by the ganglion opposite the middle, or even the anterior region of the myotome, is secondary, and that originally the ganglion and the sensory nerves were intersomitic in position, that the main sensory nerve passed out behind the myotome of its segment, and that the dorsal root has combined with the ventral root of the myotome of its own segment (that is to say, the dorsal root joins the ventral root lying in front of it).

In the head region, then, where, as van Wijhe showed, cranial nerves represent dorsal or ventral roots retaining their primitive independence, we should consider the ventral roots as lying opposite their somites, and the dorsal roots as running behind the somites to which they belong.

The Three Pro-otic Segments.—In this paper it is not necessary to enter into a very detailed account of the development and fate of the three pro-otic or pre-auditory somites. They are the premandibular, the mandibular, and the hyoid somites of Balfour; their presence has been recognised by most authors not only in the Selachians, but also in Cyclostomes, Dipnoi, Amphibians, birds, and reptiles, and mammals. They are known to give rise to the eye muscles. The ophthalmicus profundus, trigeminal, and facial nerves are considered to represent the dorsal roots of these segments, the oculomotor, trochlear, and abducens the ventral roots. My own observations fully confirm these conclusions.

The reconstructions figured on plate (Pl. 1, figs. 1, 2, 3, 5, and 7) illustrate the development of the mesoblast in the pro-otic region. The lateral plate is seen becoming compressed and eventually subdivided by the outgrowing gill-pouches. The dorsal somites become differentiated dorsally above the hyoid and the mandibular arches. At first the cavity of the somite is continued into its corresponding arch; but very soon in the hyoid, and later in the mandibular arch, this cavity is obliterated. To the account of the development of the premandibular cavity given by previous authors, I have nothing of importance to add. It has been studied in minute detail by Dohrn (5). Beyond the anterior end of the gut

and notochordal plate the tissue is continued forwards as a flattened mass underlying the brain as far as the region of the neuropore, where, at the earliest stage figured, the neural tube is still continuous with the outer epiblast (Pl. 1, fig. 1), (a). This mass of tissue develops, according to Miss Platt, into transitory "anterior head-cavities," representing a segment in front of the premandibular (22)—a conclusion which is supported by Neal (19). Yet the evidence I find in *Scyllium* seems to me against this interpretation. No trace of such an anterior somite is found in *Petromyzon* by Koltzoff (17), and, like van Wijhe, I still consider that the premandibular Al. the first (Pl. 1, fig. 19). The plate of tissue in question beyond disappears, may be considered rather as hypoblastic than mesoblastic, and might possibly represent the anterior prolongation of the notochord in *Amphioxus*. Moreover, I have elsewhere given strong evidence to support the more generally accepted view that the premandibular cavity corresponds to the first somite in *Amphioxus* (12).

A glance at Pl. 1, figs. 1 to 5, will show that from the mandibular somite backwards the regular correspondence of somites, dorsal nerve roots, and visceral pouches can be made out fairly easily. The second and third somites, however, become greatly modified, elongated, and irregularly subdivided. The cavities, which in the earlier stages may be in communication from segment to segment, may also become broken up into separate smaller spaces, some of which may disappear, while others swell up into the large head-cavities of later stages. It is these peculiarities which have led various authors (Dohrn, Killian, etc.) to hold that there are many more than three segments in front of the auditory sac. But there is much reason to believe that the appearances are due merely to the secondary subdivision of the mandibular and the hyoid somites, whose exceptional position and fate no doubt are responsible for their modification. The fact that they are stretched by the excessive cranial flexure, that they give rise not to large muscle segments but to eye muscles, and that they subsequently become for the most part drawn away into

the service of the optic capsule, would seem to sufficiently account for all the peculiarities of their development. With regard to the nerve supply of the three pro-otic somites, it is now generally agreed that the third and fourth cranial nerves represent the ventral roots of the premandibular and mandibular somites respectively. With this interpretation of van Wijhe my observations are in perfect harmony. As for the view that the sixth cranial nerve represents the ventral root of the facial segment supplying the hyoid somite, there is less unanimity. Neal (20) and Dorlin would have us believe that it is a compound nerve formed by the fusion of the ventral roots of several segments, some of which would necessarily belong originally to the post-auditory region. For this theory I can find no evidence in the development of Scyllium. Nor does Neal's contention that the abducens is a meta-otic nerve which has come to supply an eye muscle derived from a pro-otic somite seem to rest on convincing evidence. Pl. 1, fig. 7, shows that at this stage it is not so very far from the third somite it supplies. It is true that the root of the facial is relatively far forward; but this seems to be due to the cranial flexure, and an anticipation, so to speak, of the great development of the auditory sac and capsule. If this explanation proves insufficient, the two following should be considered before adopting Neal's contention. On the one hand it is possible that the anomalous position of the abducens may be due simply to the shifting backwards of its root; on the other hand, if this nerve be really compound, the fourth myotome (first meta-otic) may have contributed to the formation of the external rectus muscle. But, whatever the final verdict may be about these debatable questions, the evidence seems to be overwhelmingly in favour of there being only three pro-otic segments as originally held by Balfour.

We next have to determine the fate of the fourth somite, and to examine van Wijhe's conclusion that it corresponds to the hyoid arch. This fourth somite we may call the first meta-otic, since it first appears behind the auditory thickening

or placode, Pl. 1, fig. 2. Later on, it becomes overgrown by the auditory sac, which, as it rapidly expands, not only crushes the hinder region of the third somite in front, but almost squashes the fourth somite out of existence, Pl. 1, figs. 5 and 7. The latter breaks up into mesenchymatous tissue without yielding any distinct myotome.

In his well-known paper (26) van Wijhe states that : "Das dritte Somit befindet sich mit seiner Hauptmasse über der ersten Kiementasche, nur sein hinterer Theil erstreckt sich ein wenig weiter caudalwärts und hängt noch gerade mit der soliden Zellmasse im Hyoidbogen zusammen." . . . "Das vierte Somit liegt über der Zweiten Kiementasche und unter der Ohreinstülpung." . . . "Das fünfte Somit, dessen vorderer Theil aussen von der Anlage des Glossopharyngeus gekreuzt wird, liegt über der dritten Kiementasche." But he finds the fourth somite to be connected with the mesoderm of the hyoid arch, and the fifth somite to be connected with the mesoderm of the first branchial arch. Thus, from the fourth segment backwards, he believes the somites to be related to the arches in front of them. Consequently, since the third somite is undoubtedly related to the hyoid arch, van Wijhe finds two somites (third and fourth) connected with this arch, and associates the ninth cranial nerve with the fifth instead of the fourth somite. This strange result quite dislocates the orderly scheme of the segments, as has been already pointed out above.

My own observations do not bear out this interpretation. On the contrary, as a comparison of Pl. 1, figs. 1 to 7 shows, in *Scyllium* the visceral pouches pierce the lateral plate mesoderm in such a way that the clefts alternate with the somites, and the latter come to lie over each arch, but extend forward over the pouch in front. The fourth somite is at first distinctly connected with the mesoblast of the first branchial arch, the fifth somite with the mesoblast of the second branchial arch, and so on. Very soon, however, the somites above become disconnected from the arches below, the mesenchymatous intermediate tissue becoming diffused. Then

somites 5 and 4, and part of somite 3 also, break up; so that in an embryo some 19 mm. long the exact relation of the parts can no longer be made out, Pl. 1, figs. 7 and 8. Moreover, it is somite 4 and not somite 5 which is crossed by the glosso-pharyngeal, and it is somite 5 and not somite 6, as stated by van Wijhe, which is the first of the series of meta-otic somites to develop muscle-fibres. This is clearly shown in Pl. 1, fig. 2. In fact, my results are in agreement with those of Ziegler working on *Torpedo* (28), and like that author I am inclined to think that van Wijhe has mistaken the hinder region of somite 3 for somite 4, and consequently somite 4 for somite 5, in his description. Such mistakes are extremely difficult to avoid, and it is only by the most careful comparison of a very complete series of stages that one can trace the fate of these segments with certainty. At all events, his figures seem to agree better with the order of the segments given above than with his own tabular statement.

The Development and Fate of the Meta-otic or Occipital Somites.—Much has been written on this subject by various authors since van Wijhe (26). One may mention the works of Sewertzoff (24, 25), Froriep (6), Braus (3), and Dohrn (4).

It is important first of all to determine which is the first meta-otic segment to produce a myotome. Van Wijhe states that it is the sixth somite (overlying the fourth gill-slit). Now, my reconstructions prove beyond doubt that, as mentioned above, in *Scyllium* the fifth somite produces muscle-fibres, although its myotome never becomes fully developed, Pl. 1, figs. 2, 3, 6. Ziegler (28) likewise finds that the first myotome arises in *Torpedo* from the fifth somite, and apparently Braus (3) comes to the same result with *Spinax*.¹ We may take it, then, that the first myotome is vestigial, and develops from the second meta-otic somite in *Scyllium* and probably in other Selachians.

¹ Some confusion arises through certain authors calling the fifth somite the first and not the second meta-otic somite.

The next important point to determine is how many segments take part in the formation of the occipital region of the skull, meaning thereby the region behind the auditory sac. Van Wijhe considers that the ninth segment is the last of the head, and the tenth the first of the trunk; that the fourth and fifth form no myotomes, that the first vestigial myotome belongs to the sixth somite, for which he could find no corresponding ventral root; that the myotomes of somites 7, 8, and 9 are well developed, and each have a ventral hypoglossal root. Thus, according to our nomenclature, van Wijhe would ascribe six meta-otic segments or somites to the occipital region in *Scyllium* and *Pristinurus*. Various authors who have worked at *Torpedo* have described a larger number of meta-otic segments in this fish: Sewertzoff, 10; Froriep, 13; and Dohrn, 11. But, as already stated above, we believe these discordant results are due to the secondary breaking-up of the somites into pieces which have been reckoned as segmental. Ziegler, indeed, has brought *Torpedo* into conformity with other Elasmobranchs.

Fürbringer, in his monograph on the hypoglossal nerves (7) developing Gegenbaur's views, maintains that a large number of Neocranial segments have been added to the head behind the original Palæocranial region to which the vagus is supposed to belong. Eight such trunk segments, designated by the letters *s-z* from before backwards, are assumed to have thus become assimilated to the head, together with their nerves (of the same nature as the spinal nerves). These neocranial somites and their nerves are further supposed to become progressively reduced, so that in the adult only those representing the last three letters of the alphabet, *x*, *y*, *z*, remain in *Scyllium*. Braus (3), in an elaborate study of the development of the occipital region in *Spinax* and other Selachians, attempts to support this theory on embryological grounds. According to him, the first vestigial myotome is produced from the fifth somite and the first complete myotome from the sixth somite (= *u*); but all the myotomes in front of *x* are supposed to disappear in the course of develop-

ment. Braus describes a process of shifting forwards of the myotomes to a position below the vagus-root and behind the auditory capsule where they degenerate. But what definite evidence is there that such a procession of myotomes which plunge one after the other below the capsule and vanish in a cloud of mesenchyme really occurs? Neither Dohrn (4) nor myself can find any. On the contrary, there is good reason to believe that for the most part myotomes once laid down persist, and that the chief change that takes place in the course of ontogeny is the crushing of the anterior myotomes owing to the growth backwards of the auditory sac and capsule, of the vagus, and of the gill-sacs.

In his careful description of the development of the occipital somites in *Acanthias*, Hoffmann (15) follows van Wijhe, states that somites 4-8 lie each above the five branchial slits, that somite 6 produces the first muscle, which degenerates later, that somites 9 and 10 form the last occipital segments, that myotomes of somites 7-9 are cut in half by the vagus root growing backwards, and that the ventral roots of segments 7, 8, and 9 alone persist. He attributes ten segments to the head region, and assumes that the eleventh, with a complete spinal nerve, is the first segment of the trunk.

Turning now to our reconstructions of *Scyllium*, we find that the first few somites behind the auditory capsule undergo different changes and suffer different fates. The first (fourth somite), crossed by the rudiment of the glosso-pharyngeal nerve, forms no muscle, and soon breaks up into mesenchyme. For a long time its posterior upper extremity retains an epithelial structure, and can be recognised behind the glosso-pharyngeal (Pl. 1, figs. 4, 5, 6). The next meta-otic somite (S_5) lies at first under the vagus root, and is crossed by the first vagus branchial nerve and ganglion (Pl. 1, figs. 4, 5, 6) later on it spreads out, acquires a lobed, irregular dorsal edge, and projects beyond the vagus root both in front and behind (Pl. 1, figs. 6, 8, 11). Muscle-fibres develop in its hinder region, forming the first meta-otic myotome. In early stages

no ventral root can be seen supplying this myotome. According to van Wijhe and later authors the first meta-otic myotome degenerates in the course of ontogeny; but, although I have devoted much time and the greatest care to the settlement of this point, I have never been able to make absolutely certain as to its fate. In stage J (Pl. 1, figs. 5, 6) *S* 5 can be clearly made out, and is still plainly related to the second branchial arch; owing to its position below the vagus it cannot form a complete myotome with a large dorsal process such as grows up from the sixth and succeeding somites. That the sixth somite forms a complete myotome passing up dorsally behind the vagus is clear from a comparison of Pl. 1, figs. 1-11, and Pl. 2, fig. 19. Although in later stages the upper dorsal region of this myotome becomes cut off by the vagus root from the lower ventral portion (Pl. 1, figs. 9 and 11), yet it persists throughout development, stretching farther and farther forward over the occipital region of the skull. The ventral root supplying this second meta-otic myotome (*S* 6) develops early (Pl. 1, fig. 10), and later, piercing the skull, passes into the vagus groove (Pl. 2, fig. 17). It is the nerve *y* of Fürbringer. The nerve *z* of Fürbringer passes through a foramen in the occipital region further back, and supplies the complete myotome of somite 7, dividing into a dorsal and a ventral branch (Pl. 2, fig. 17). The myotome of the next somite, 8, is supplied by the first spinal nerve, issuing between the occipital arch and the first neural arch (Pl. 2, figs. 15-18). If the enumeration of the segments given above is correct, it follows that there are only four meta-otic segments, of which the last three are represented by muscles and nerves in the full-grown fish. But the numbering all depends on the accurate determination of the small ventral slip of muscle lying entirely below the vagus root. Is this really in later stages the persistent remains of the myotome of the second meta-otic somite (*S* 5), or has this muscle degenerated, shifted forwards, and been replaced by that of the third meta-otic somite (*S* 6)? After a most careful consideration

of the facts as displayed in the series of reconstructions here figured, and of a large number of sections and whole preparations of intermediate stages not figured, I have come to the conclusion that the first interpretation is correct. During the earlier stages (Pl. 1, figs. 5, 6, 7), when the original relation of the second meta-otic somite to the first branch of the vagus is still easy to make out, it seems clear that the somite does not really alter its position fundamentally; its hinder upper corner always can be seen to pass just behind the vagus root, and sometimes forms here quite a considerable dorsal process (Pl. 1, fig. 8). Nor can any distinct signs of degeneration be detected in its muscle before cartilage is formed. In quite late stages the minute slip of epibranchial muscle it forms is either difficult to distinguish from that of the next segment (*S* 6), or has disappeared. The ventral nerve root of the first myotome (*S* 5) cannot be detected in quite early stages. It seems to develop late, and is sometimes clearly visible when cartilage has begun to form (Pl. 2, fig. 15). In quite late stages it is seen to issue through a foramen as a slender nerve which joins the next behind. It seems to me probable that its comparatively large size in some of these later stages is due to its contributing to supply the hypoglossal muscles, some of which have probably been derived from the fifth somite.

* Since one cannot follow the development of a given segment through successive stages in the same individual, it is impossible to remove all doubt as to the identification of a segment. But if the interpretation given above is wrong, and if the first meta-otic myotome really disappears in the course of ontogeny, as other authors have asserted, then this disappearance must take place late or very early. (It would seem that the belief in the early degeneration of the first myotome is partly due to the miscalculation of the segments made by van Wijhe and already discussed above.) In that case the somites numbered 5, 6, 7 in Pl. 1, figs. 7-11 should be numbered 6, 7, 8. There can, I think, be no doubt whatever that such a process of degeneration of myotomes

goes no further, if it takes place at all; for there is every reason to believe that these three somites are the same as the three numbered 5, 6, 7 in figures of later stages (Pl. 2, figs. 15-18). They can be followed step by step with comparative ease. In the latest stages studied, when cartilage has developed and the occipital region has practically acquired the adult structure, the spinal nerve of the second trunk segment is found provided with normal dorsal and ventral roots and a well-developed ganglion (Pl. 2, figs. 17, 18), while the first spinal nerve has a large ventral root, but only a vestige of a ganglion, and usually no distinct dorsal root. From this point forwards no trace of dorsal ganglia or roots can be found in late stages. Turning to earlier stages, we find that although transitory rudiments of ganglia are formed in all the anterior segments, the eighth somite never at any time has a fully-developed ganglionic rudiment. The history of the ganglia, then, affords evidence that the somite numbered 8 in my figures is the first trunk segment. The evidence, however, is not absolutely conclusive, since the rudiments are subject to much individual variation and there is a gradation in size from before backwards.

But in embryos 26 mm. long (Pl. 2, fig. 12), where the first traces of procartilage can be distinguished, the identity of the segments can be clearly made out. From that time onwards the fate of the myotomes can be traced with certainty, and there is neither a degeneration of muscles in front nor an assimilation of new myotomes behind.

To sum up the foregoing observations on the development of the meta-otic somites and nerves: In the adult *Scyllium canicula* the second trunk segment has a complete myotome and a complete spinal nerve, with dorsal and ventral root and a ganglion. In quite late stages the first trunk segment has a complete myotome, but a spinal nerve in which the dorsal root and its ganglion have been reduced to a mere vestige, if present at all (Pl. 2, fig. 17). The fully developed ventral root of this first spinal passes out between the occipital arch of the skull and the first neural arch of the vertebral column.

Two occipital nerves are always found piercing the hinder region of the skull. The larger and more posterior issues through a foramen lying on the inner aspect of the skull about halfway between the occipital margin and the vagus foramen. This nerve (*z* of Fürbringer) supplies the last occipital myotome (*S* 7). The foramen for the more anterior nerve lies below the vagus foramen; the nerve supplies the penultimate occipital myotome, complete, but subdivided by the vagus root into dorsal and ventral portions (Pl. 2, fig. 16). According to Fürbringer (7), a third nerve passes out still further forward. I find that it occurs in some but not in all adults. It seems to develop late, and a mere trace of it can be detected in a stage 33 mm. long, while it is clearly seen in the later stage shown in Pl. 2, fig. 17. Since the last two occipital nerves can be identified for certain from the adult to the 26 mm. stage, when procartilage is only just coming into evidence, it may be concluded with practical certainty that this slender and inconstant nerve root is that of the first of the three occipital myotomes, which is never completed dorsally, being placed below the vagus root and crossed by the first branchial branch of the vagus. According to my observations this first meta-otic myotome, which may or may not persist in the adult, develops from the fifth somite (second meta-otic), and never moves much from its place of origin. No muscle at all is developed in the fourth somite, which is crossed by the rudiment of the glosso-pharyngeal and crushed by the enlarging auditory sac. The series of meta-otic somites is regularly related to the gill-slits, one being placed originally above each branchial slit from the first to the fifth, and connected with the following branchial arch. There are thus five somites in the branchial region. The last of these, situated above the fifth branchial slit (sixth gill-slit), and related to the fifth branchial bar (seventh visceral bar), has a myotome supplied by the first spinal nerve and therefore belonging to the trunk, if we draw the distinction between the head and the trunk at the occipital joint. Excepting for the first meta-otic myotome (*S* 5), which seems to disappear

in many individuals, there appears to be no further degeneration of myotomes at any stage, nor is there any evidence of the shifting forwards of myotomes or disappearance of successive segments such as has been described by many authors.

Concerning the nerves of the occipital region, it should be noticed, in addition to what has been mentioned above, that no ventral root ever appears belonging to the glosso-pharyngeal (S 4). The four branchial branches of the vagus with their epibranchial placodes represent the dorsal roots of meta-otic segments 5, 6, 7, 8. Therefore to the first of these belongs the vestigial and inconstant ventral root described above (p. 15), while to the second and third correspond the two posterior occipital nerves which pierce the skull. The ventral root of the eighth segment containing the fourth vagus branch is the first spinal nerve. Only incomplete dorsal roots and ganglia are developed in these segments, but they are all quite obvious at certain stages in ontogeny (Pl. 1, figs. 6, 11), disappearing later completely in segments 5, 6, and 7, and remaining only as a mere vestige in segment 8 (Pl. 2, fig. 17). Without entering into a detailed discussion of the structure and origin of the vagus nerve, so well dealt with by Johnston (16), it may here be pointed out that, while the embryological evidence in *Scyllium* (and especially in *Petromyzon* — see Koltzoff (17)) is definitely against the view of Gegenbaur that the vagus has been formed by the gathering together of a number of complete segmental nerves, yet it is in favour of the view that the vagus is a complex nerve, formed, not so much with the help of a longitudinal collector, as held by Koltzoff and Johnston, as by the gathering together of only certain portions of segmental nerves (four in *Scyllium*), leaving behind other portions or components, which remain as the incomplete and more or less transitional roots and ganglia of the vagus region. This theory seems to be the only one which will account for the facts, and at the same time explain the formation of the vagus without the disturbance either of the central or of the peripheral connections of the nerves; for the gathering

and sorting out of the components probably takes place at an early stage when the neural crest is still, in this region, continuous.

The Development of the Cartilaginous Elements.—My observations on the development of the cartilages of the skull in *Scyllium* differ in no very important respect from those of Sewertzoff on the skull of *Acanthias* and *Pristiurus* (25). The first sign of the appearance of the skull is in the form of a sheet of dense mesenchyme extending on either side of the notochord. From the level of somite 4 it thins out forwards, reaching to the infundibular region (Pl. 1, fig. 9). No distinct signs of segmentation are any longer visible at this stage in this tissue which, however, is doubtless derived from the sclerotomes of segments 4 and 3, and perhaps also of segments 2 and 1. Two outgrowths seem to mark the original position of sclerotome 4 below the glosso-pharyngeal nerves (Pl. 1, figs. 10, 12). The scleromeres are formed further back in segments 5, 6 and 7, just as they are in the trunk (p. 6) by a condensation of mesenchyme in the hinder region of each segment and stretching outwards behind the corresponding nerve and myotome (Pl. 1, figs. 10, 11). The thickened posterior edge of the parachordal sheet doubtless represents the scleromere of segment 4 (first meta-otic). In later stages the parachordal plate and occipital scleromeres become more and more developed, until the latter fuse with each other and with the plate. In an embryo 26 mm. long the first signs of procartilage are visible. Staining with thionin brings out behind the wide parachordal plate (Pl. 2, fig. 12) two occipital arches rising from the floor of less dense tissue, and a more posterior accumulation of cells near the notochord representing the centrum. This element, probably derived from the sclerotome of the eighth segment, gives rise to the occipital condyles, if we may designate by this term the paired processes projecting backwards towards the centrum of the first vertebra in the adult. Very soon all these occipital elements become indistinguishably fused to the parachordal plate (Pl. 2, figs. 13, 14).

The two rudiments of occipital arches mentioned above arch over the last occipital nerve in the 26 mm. embryo (Pl. 2, fig. 12). Later on they together form on each side the large cartilaginous arch which grows upwards surrounding the foramen magnum, completes the side walls of the occipital region, abuts against the auditory capsule in front, and finally fuses with it (Pl. 2, figs. 13-18). Van Wijhe (27) considers that this large arch represents a single neural arch of the vertebral column (pierced by a ventral root in *Acanthias*). But the early relation of the two pillars of the arch to the enclosed nerve and to the septa seems to prove that the cartilaginous occipital arch is composed of two elements each equivalent to a neural arch and belonging to segments 6 and 7 (Pl. 2, figs. 12, 14). Further forward similar arches are indicated (Pl. 2, fig. 14) by uprisings of the parachordal plate, which eventually surround the anterior occipital nerves and complete the sides of the cranium behind and below the auditory capsule (Pl. 2, fig. 17).

Since the last occipital segment corresponds to the seventh somite lying over the fourth branchial slit and fourth branchial bar supplied by the third branch of the vagus, it is clear that the last slit and vagus branch belong morphologically to a segment behind the posterior limit of the occipital arch in *Scyllium* (the condyles, however, probably belong to the eighth segment). This discrepancy between the skull and the other organs of the head is not unusual among Vertebrates. I have elsewhere shown that in *Urodeles* the vagus and gill-slits extend behind the occipital segments (10 and 11), and in *Petromyzon* the discrepancy is, of course, still more pronounced. The fact is that the process of cephalisation has to some extent been independently carried out in the visceral and in the cranial elements. As Koltzoff (17) points out, a different limit may be assigned to the head according as we take one system or the other as our criterion. To avoid the somewhat paradoxical conclusion that the head region extends into the trunk, it would be advisable for practical purposes to use the term "cranial

region" for the segments as far as the hind limit of the rigid skull at the occipital joint, and "visceral region" for the segments reaching back to the last gill-slit and vagus bronchial nerve. Thus in *Scyllium* there would be seven cranial and eight visceral segments, in *Siredon* six cranial and seven visceral segments, while in *Petromyzon* there would be ten visceral but only four cranial segments. According to Brans (3) the last occipital and the first trunk spinal nerves are always the same in the *Selachians*, but Rosenberg (23) in *Carcharias* and van Wijhe in *Acanthias* and *Heptanchus* (27) believe a late addition is made to the skull by the assimilation of one or more vertebral segments. In *Scyllium* no such addition takes place, for the centra of the first two trunk segments are always separate from their neural arches (Pl. 2, fig. 17), differ in this respect from those behind, and can be detected in consequence even in embryos only 26 mm. long (Pl. 2, fig. 12).

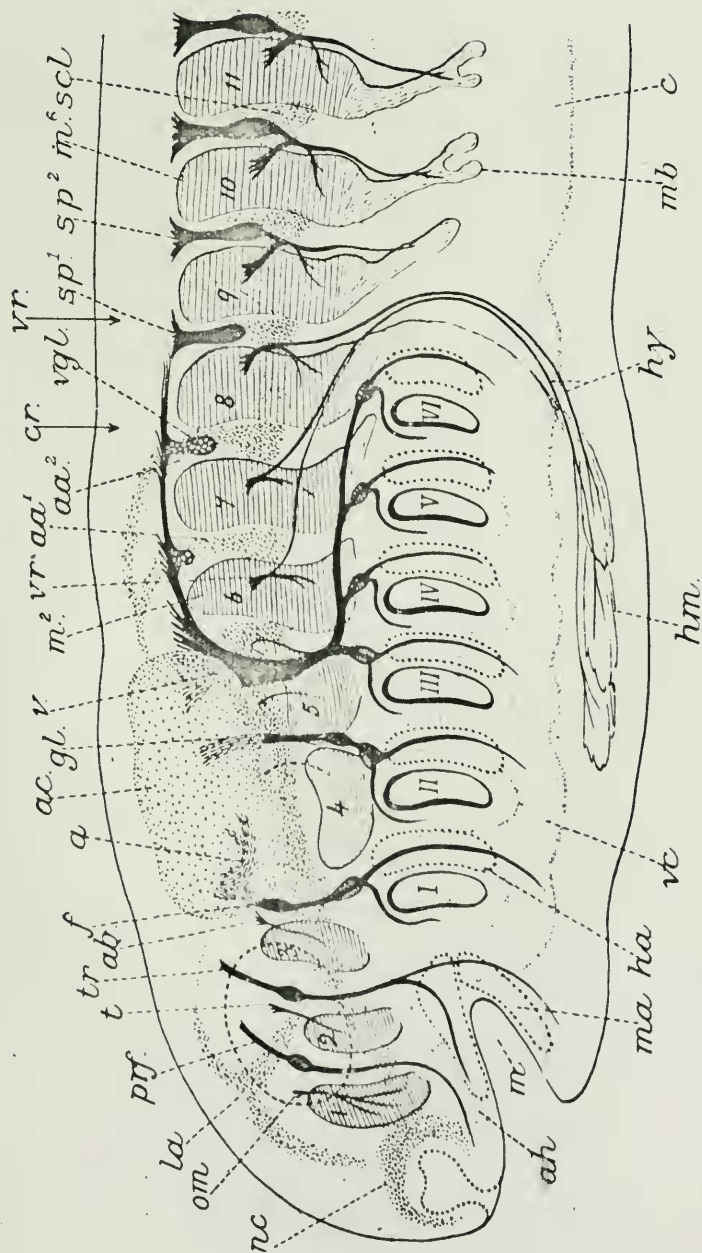
Although this paper deals chiefly with the occipital region, a few words may be added about the development of the rest of the skull. The essential facts have already been described by Sewertzoff (24), and in a valuable preliminary note without figures by van Wijhe (27). The trabeculae in an embryo 26 mm. long are scarcely discernible except as a slightly denser region of mesenchyme on either side of the infundibulum. In the 33 mm. stage figured (Pl. 2, figs. 13-16) they appear as distinct cartilage rods expanding in front into a procartilaginous sheet, which spreads out between the orbit and the nasal capsule—the first indication of Sewertzoff's ethmoid cartilage. At no stage in development do I find the trabeculae bent down at right angles to the parachordal plate as figured by Sewertzoff, but always from the first more nearly in the same plane (Pl. 2, fig. 14). They soon join and fuse with the extreme anterior corner of the parachordal plate, below the ring which grows out from the plate to surround the anterior carotid (Pl. 2, figs. 14, 18). In front the trabeculae join in the middle line (Pl. 2, fig. 18), and are continued forward and upward into the nasal septum. A film

of procartilage continuous with the upper edge of the septum extends over the nasal sac on either side, and develops into the overhanging nasal capsule completed behind by the expanding ethmoid wing. Above, in the inner wall of the orbit, arise the alisphenoid cartilages of Sewertzoff (sphenolateral of Gaupp (8), lamina antotica of van Wijhe). At first separate, they soon join the parachordals, spread out into a thin sheet of procartilage dorsally, and eventually become continuous with the auditory capsule behind and the ethmoid cartilage in front. Originally situated between the oculomotor and the trigeminal nerve, the lamina antotica forms the greater part of the wall of the orbit and surrounds the nerve exits in this region.

The development of the auditory capsule is of some importance. It is formed in the layer of tissue immediately surrounding the sac, faithfully following the folding of the sac when the semicircular canals begin to appear (Pl. 2, figs. 13-16). Cartilage develops much later in the capsule than in the parachordal plate or occipital arch. From the very first

Diagram of the segmentation of the head in *Scyllium canicula*: *C.R.* Limit of cranial region. *V.R.* Limit of visceral region. I-VI. Gill-slits. 1-11. Somites, prootic from 3 forwards, and metaotic from 4 backwards. *a.* Auditory nerve. *ab.* Abducens nerve. *ac.* Auditory capsule. *ah.* Anterior head-cavity. *c.* Coelom in lateral plate mesoblast. *f.* Facial nerve. *gl.* Glosso-pharyngeal nerve. *ha.* Hyoid cartilaginous arch. *hm.* Hypoglossal muscles from myotomes of somites 6, 7, 8. *hy.* Hypoglossal complex nerve. *la.* Lamina antotica. *M.* Mouth. *m².* Second metaotic myotome. *m⁶.* Sixth metaotic myotome. *ma.* Mandibular cartilaginous arch. *mb.* Muscle-bud to pectoral fin. *nc.* Nasal capsule, continuous with trabecula behind. *aa.¹* and *aa.²* First and second occipital arches of segments 6 and 7. *om.* Oculomotor nerve. *prf.* Profundus nerve. *scl.* Sclerotome of segment 10. *sp.¹* Vestigial dorsal root and ganglion of first spinal nerve. *sp.²* Second spinal. *t.* Trochlear nerve. *tr.* Trigeminal nerve. *v.* Complex root of vagus nerve. *vgl.* Vestigial dorsal root and ganglion of segment 7. *vc.* Ventral coelom extending up each visceral bar. *vr.* Ventral nerve-root of segment 6, supplying second metaotic myotome and hypoglossal muscle. The myotomes are longitudinally striated, the nerves black, and the scleromeres dotted. The cartilaginous visceral arches are represented by dotted outlines, also the optic capsule and the nasal sac.

TEXT-FIG. 1.



(Pl. 2, fig. 12) the slightly denser layer of tissue from which the capsule arises seems to be continuous ventrally with the parachordal plate, as described by Sewertzoff. This continuity is between the facial and the glosso-pharyngeal nerves (Pl. 2, fig. 12); but as the capsule expands backwards it passes above the glosso-pharyngeal and vagus, leaving a considerable gap through which these nerves pass out between the capsule and the plate. Later this gap forms the vagus groove (Pl. 2, figs. 15, 17). Cartilage spreads from two pillars rising up from the parachordal plate, one passing up the anterior outer corner of the capsule, and the other up its inner wall (Pl. 2, figs. 14, 18, *po.*, *p.*).

SUMMARY.

Although the observations recorded above bring out no striking novelty, they will, I think, be useful in completing our knowledge of the development of the head region in Elasmobranchs, in clearing up some obscure points, and in settling certain questions about which there has been much uncertainty and controversy.

In a trunk segment of *Scyllium* the ventral root of the spinal nerve is mid-segmental or somitic, and the dorsal root intersegmental or intersomitic in morphological position. To form a mixed spinal nerve, the ganglionated dorsal root joins the ventral root in front, and the main branch passes outwards in the septum behind its myotome. In the head region, where the roots retain their original independence, the dorsal roots, therefore, are also morphologically situated behind the somites to which they belong.

There are three pro-otic segments, corresponding to the profundus, trigeminal, and facial nerves. Somite 1 is pre-oral, somite 2 lies above the mouth and is related to the mandibular bar. Somites 3 to 8 lie above each of the six gill-slits, and are related to the hyoid and five branchial bars. The three pro-otic somites are supplied by the oculomotor trochlear, and abducens nerves. The first meta-otic segment, with the glosso-pharyngeal nerve, contains somite 4, which

produces no myotome and has no ventral root. Three more meta-otic somites, supplied by the occipital ventral roots, and corresponding to the first three branchial branches of the vagus, complete the cranial region. The eighth somite belongs to the first spinal nerve, of which the dorsal root is absent or vestigial in later stages, and to the fourth branch of the vagus.

The vagus nerve has been formed by a partial gathering forward of components of four dorsal roots, without breaking either their central or their peripheral connections. The visceral region of the head extends one segment farther back than the cranial region, and the hind limit of the head differs according as we choose to determine it by the extent of the cranial or the visceral cephalisation. There is little or no degeneration or shifting forwards of myotomes behind the auditory capsule.

Segments 3 and 4, and possibly also 1 and 2, contribute to the formation of a basal mesenchymatous sheet below the hind brain, from which develops the parachordal cartilaginous plate on either side of the notochord. Scleromeres from segments 5, 6, and 7 become added to these plates behind, and the "condyles" seem to be formed from segment 8. The lateral and dorsal walls of the occipital region are formed by the upgrowth of elements corresponding to the neural arches. The two posterior of these elements, belonging to segments 6 and 7, combine to form the large occipital arch, which fuses with the auditory capsule. The neural arches develop in the denser posterior region of the sclerotomes; and in the first two segments of the vertebral column they are separate from the centra. The auditory capsule from its first origin is continuous with the parachordal plate between the facial and the glosso-pharyngeal nerves. It grows backwards, covering the latter, the vagus, and the occipital nerves. The trabeculae develop later than the parachordals, with which they soon fuse; they meet in front to form the median nasal septum, and develop large ethmoid wings which contribute to the nasal capsule together with the septum. On either side a

lamina antotica arises separately in front of the trigeminal nerve, soon fuses with the parachordal, expands upwards, and eventually forms the greater part of the wall of the orbit and upper roof of the skull.

July 24th, 1917.

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EXPLANATION OF PLATES 1 AND 2,

Illustrating Mr. Edwin S. Goodrich's paper "On the Development of the Segments of the Head in *Scyllium*."

EXPLANATION OF LETTERING.

a. Anterior tissue (ant. head-cavity of Platt). *ab.* Abducens nerve. *ac.* Auditory capsule. *al.* Alimentary canal. *als.* Alisphenoid cartilage or lamina antotica. *ant. c.* Anterior carotid. *ar.* Artery. *as.* Auditory sac. *Ba.*¹⁻⁵ Branchial bar 1-5. *bh.* Basihyal. *bp.* Basal parachordal plate. *c¹* Centrum of first trunk segment. *c. Ba.* Cartilaginous branchial arch. *cv.* Posterior cardinal vein. *da.* Dorsalaorta. *f.* Facial nerve and its rudiment. *eg.* External gill. *eth.* Ethmoid cartilage. *ggl.* Spinal ganglion. *gl.* Glosso-pharyngeal nerve and its rudiment. *gp.*¹⁻⁶ Gill-pouch 1-6. *H.* Hyoid bar. *hm.* Hyoman-

dibular cartilage. *ht.* Heart. *hy.* Hypophysis. *lp.* Lateral plate mesoderm. *m.* Myotome. *m.¹⁻¹⁰* First and succeeding myotomes. *ma.* Mandibular artery. *mc.* Mandibular cælotomic canal. *md.* Mandibular bar. *mdc.* Mandibular cartilage. *na.* Neural arch. *nac.* Nasal capsule. *nc.* Nerve cord. *ns.* Nasal septum. *nt.* Notochord. *oc.* Occipital condyle. *oca.* Occipital arch; *oca¹* and *oca²* its first and second pillars. *ocm.* Oculomotor nerve. *opn.* Optic nerve. *p.* Dorsal process of parachordal plate. *pc.* Pericardium. *pn.* Pronephros. *po.* Outer dorsal process of parachordal plate. *post. c.* Posterior carotid. *ppl.* Basal parachordal plate. *pqc.* Palatoquadrate cartilage. *ps.* Posterior denser region of scleromere. *S.¹⁻¹⁰* First to tenth somite. *sa.* Segmental artery. *sn.* Sensory nerve from dorsal ganglion. *sof.* Superior ophthalmic branch of facial nerve. *sofg.* Superior ophthalmic branch of trigeminal nerve. *sv.* Segmental vein. *tg.* Trigeminal nerve and its rudiment. *tra.* Trabecula cranii. *tro.* Trochlear nerve. *v.* Vagus nerve. *v.¹⁻⁴* Its four branchial branches and ganglia. *vr.* Cut root of vagus. *vggl.* Vestigial ganglion of first spinal nerve. *vgr.* Vagus groove. *va.* Vein. *vr.* Ventral root of spinal nerve.

[All the figures are of various stages of *Scyllium canicula*, L. Figs. 1, 2, 3, 5, 13-17 are reconstructed on median longitudinal vertical sections, and the outer epidermal covering is, for the most part, omitted. The somites and other mesoblastic structures are drawn in red on Plate 1, myotomes being indicated by horizontal strokes, mesenchyme and sclerotomal tissue by dots. Cartilage is coloured purple, and pro-cartilage is represented in purple dots on Plate 2.]

PLATE 1.

Fig. 1.—Left side view of the anterior region of an embryo at stage F.

Fig. 2.—Similar view of stage G.

Fig. 3.—Stage G, rather later than Fig. 2. Inner view of right half of embryo.

Fig. 4.—Stage I (about 6 mm.). Dorsal view, the left half at the level of the middle of the notochord; the right half cut more dorsally. On the right the roots of the glosso-pharyngeal and vagus nerves have been completely reconstructed to show their position over the somites.

Fig. 5.—Stage J (about 7 mm.). Left side view, with the lateral wall of the gill-bars shaved off, exposing the five gill-pouches.

Fig. 6.—More enlarged inner view of somites 4-11, with the related nerve roots, etc., of the right side of the same embryo.

Fig. 7.—Left side view of the anterior region of an embryo 10 mm. long. The side of the body has been cut away more deeply than in Fig. 5.

Fig. 8.—Embryo 19 mm. long. Reconstruction of the nervous system, and myotomes of the auditory and occipital regions of the right side.

Fig. 9.—Embryo 26 mm. long. Reconstruction of the auditory sac, nervous system, myotomes, etc., of the left side of the auditory and occipital regions. The dense mesenchyme or blastema of the basal parachordal plate and more posterior scleromeres is indicated by dots.

Fig. 10.—Dorsal view of a slice of the left side of the occipital region reconstructed from horizontal sections of an embryo 20 mm. long.

Fig. 11.—Portion of the nervous system, somites, etc., of the left side of an embryo of stage J (of Balfour). The slice includes only the roots of the glosso-pharyngeal and vagus.

PLATE 2.

Fig. 12.—First appearance of the skeleton of the head, embryo 26 mm. long, in the form of procartilage indicated by dots. Dorsal view (slightly oblique) reconstructed from horizontal sections. On the left the nervous system is more completely shown. On the right the auditory capsule is indicated.

Fig. 13.—Embryo 33 mm. long. Right-side view of head region with nervous system and skeleton.

Fig. 14.—More enlarged view of the skull, showing the occipital arch, parachordal plate, trabecula, and alisphenoid cartilages. The procartilaginous extensions of the two latter are cut off.

Figs. 15 and 16.—Two views of the occipital region of the 26 mm. embryo of Fig. 13 more enlarged. Figs. 15 represents a slice showing the skeleton and nerve roots. Fig. 16 a thicker slice including more of the skull and nerves, and the myotomes. The near-cut surfaces of the cartilages are dotted.

Fig. 17.—Thick slice of the left occipital region of an advanced embryo with fully developed skeleton. The occipital region of the skull, the first three segments of the vertebral column, and the nerves are shown. The three occipital nerves are represented hanging down from the vagus groove and outside the cartilage.

Fig. 18.—Dorsal view (slightly oblique) of the head skeleton, nerves, etc., of an embryo about 33 mm. long, but more advanced than that shown in Fig. 13. On the left the nasal capsule, alisphenoid cartilage, auditory capsule, and vertebral column are completely reconstructed; the cranial and spinal nerves, and the myotomes are also shown. On the right side, while the alisphenoid cartilage and auditory capsule have been removed, the mandibular and hyoid arches are included, and also some arteries.

Fig. 19.—Left side view of the anterior region of an embryo of stage G, drawn from a specimen stained and mounted whole.

Figs. 20 and 21.—Reconstructions, somewhat diagrammatic of the right side of some trunk segments of stage J, Fig. 20, and stage N, Fig. 21; showing the relation of the parts to each other.

Figs. 22, 23, and 24.—Three horizontal sections showing the relation of the various parts of the segments on the left side. Fig. 22 represents the most dorsal, and Fig. 24 the most ventral section of the same segments.

[NOTE.—The embryonic stages of the Dog-fish indicated by capital letters in this memoir are those so indicated in the well-known classification of stages used by Balfour.]